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Trigastrotheca laikipiensis sp. nov. (Hymenoptera: Braconidae): A New Species of Brood Parasitic Wasp that Attacks Foundress Queens of Three Coexisting Acacia-ant Species in Kenya

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Abstract.—***Trigastrotheca laikipiensis*** **Quicke sp. nov.**, from Kenya, is described and illustrated. It is shown to be an ant brood parasite in claustral colonies of three acacia ant species which inhabit *Acacia drepanolobium* thorns. The larvae of *T. laikipiensis* sp. nov. consume ant eggs, larvae and pupae. Brood parasitism was found in up to 20% of *Crematogaster mimosae* and *C. nigriceps*-occupied thorns, but was far rarer in the case of *Tetraponera penzigi*. *Crematogaster* foundress queens actively defend *T. laikipiensis* sp. nov. larvae, cocoons and recently eclosed adults.

Two new combinations and one new name are proposed: *T. inermis* (Guérin-Méneville) **comb. nov.** (on authority of C. van Achterberg) [*Spinaria inermis* Guérin-Méneville, 1848], *T. romani* **nom. nov.** [= *Coelodontus costator*: Roman; = *Ichneumon costator* Thunberg, 1822, a junior homonym of *Ichneumon costator* Donovan, 1810] and *T. rugosa* (Szépligeti) **comb. nov.** [= *Bracon rugosa* Szépligeti; = *K. rugosa*: Quicke & Koch, 1990].

Key words.—*Trigastrotheca, Kenema*, brood parasitism, *Crematogaster, Cordia*, ant colony founding, new combination, new name

Many upland savannas on black cotton soils in East Africa are dominated by a single species of swollen thorn ant-acacia, *Acacia drepanolobium* (Harms) Sjøstedt (Young et al. 1998, Taiti 1992). Within the canopy layer of this relatively simple plant community, up to four species of specialized, symbiotic acacia-ants coexist at fine spatial scales, despite the fact that *A. drepanolobium* host trees are a limited resource for which symbiotic ant colonies compete intensively (Hocking 1970, Palmer et al. 2000, 2003, Palmer 2003, Young et al. 1997). Three of these acacia-ant species (*Crematogaster mimosae* (Santschi), *C. nigriceps* (Emery), and *Tetraponera penzigi* (Mayr)) produce young queens which attempt to initiate new, independent claustral colonies (i.e. ones made by a newly mated queen who seals herself in a thorn to raise her first brood) within swollen thorns on *A. drepanolobium* trees that do not have any other active, mature ant colony. These colonization targets are usually small saplings (< 0.6 m tall), but may occasionally be larger trees recovering from disturbances such as fire or prolonged drought (Stanton et al. 2002). Competition among foundress queens for colonizable swollen thorns is intense, with almost 80% of foundress mortality in claustral colonies attributable to combat with other queens trying to colonize the same swollen thorn (Stanton et al. 2002, Stanton et al. in press). Another major source of failure for claustral foundresses is brood parasitism by a previously undescribed braconid wasp (*Trigastrotheca laikipiensis* sp. nov. Quicke), which is the focus of this paper, and which could potentially have significant effects on this guild of acacia-ants.

OBSERVATIONS

At our primary study site, the Mpala Research Centre in the Laikipia District of Kenya (0°17′ N, 37°52′ E; approximately 1800 m elevation), we carefully searched for small saplings of *A. drepanolobium* that were potential colonization targets for foundress queens in June–July of 2001 and 2004. After opening up swollen thorns in which foundresses had sealed themselves and their brood, we examined the brood under a microscope to search for evidence of *T. laikipiensis* sp. nov. parasites. We were unable to identify eggs or very young larvae of the parasitic wasp, but older wasp larvae could be distinguished from ant brood by their more tapered shape. These wasp larvae were often found feeding on ant eggs (Fig. 1a), larvae (Fig. 2), and pupae. The parasitoid cocoons are typically formed free inside the colonies (Fig. 1b). All stages of the parasitoids were apparently accepted by host foundresses, the latter actively guarding wasp larvae, cocoons/pupae and even recently eclosed wasp adults, as though they were legitimate offspring, when challenged by one of us (MLS) (see Fig. 1b).

Ninety percent of claustral colonies founded by a singleton queen lose all of their brood if parasitized by a wasp that reaches late instar stages of development, whereas approximately half of pleometrotic (i.e. colonies founded by more than one queen) groups of *C. mimosae* foundresses produce mature brood even if hosting a successful wasp parasitoid. At two sites within our study area, parasitism by *T. laikipiensis* sp. nov. ranged from 5% to >20% on claustral colonies of *C. nigriceps* (n = 511), and from <5% to 17.5% on *C. mimosae* (n = 475) (Stanton et al. in press). Parasitism by *T. laikipiensis* sp. nov. on claustral colonies of *Tetraponera penzigi* was rare in all of our samples (n = 231), suggesting either that the wasp specializes on *Crematogaster* in this system, or that *Tetraponera* foundresses tend to be intolerant of its presence. It is likely, however, that these parasitism rates are underestimates because *Trigastrotheca laikipiensis* sp. nov. eggs were never recognized. Some of the braconid brood parasitoids are themselves attacked by a still-unidentified endoparasitoid eurytomid wasp.

In most cases only a single *Trigastrotheca* larva was observed in a nest, but on a few occasions (< 5% of observations) two parasitoids were present. However, because *Trigastrotheca* eggs and early larvae have not been recognized, this estimate of multiple parasitism is almost certainly an underestimate. On two occasions, out of many hundreds, one cocoon and one late instar parasitoid larva were observed in a colony, indicating that two *T. laikipiensis* sp. nov. can probably successfully complete development, at least occasionally.

TAXONOMY

Trigastrotheca Cameron

Trigastrotheca Cameron (type species *Trigastrotheca trilobata* Cameron, 1906)
Coelodontus Roman (type species *Ichneumon costator* Thunberg, 1822) synonymized by Quicke (1987), but see below.
Odontopygia Enderlein (type species *Odontopygia tridentata* Enderlein {1918} 1920)
Kenema van Achterberg [type species *Kenema quickei* van Achterberg (1983) synonymized by Quicke (1987)].

Trigastrotheca is a small genus of moderately small parasitic wasps found predominantly in Africa but also known from Australia (Quicke and Ingram 1993) and the Indo-Australian region. They are currently placed in the Braconini and are characterized by the modified 5th metasomal tergite of the female, which has strong submedial posterior emarginations that define a medial and pair of sublateral points. The genus may be identified using

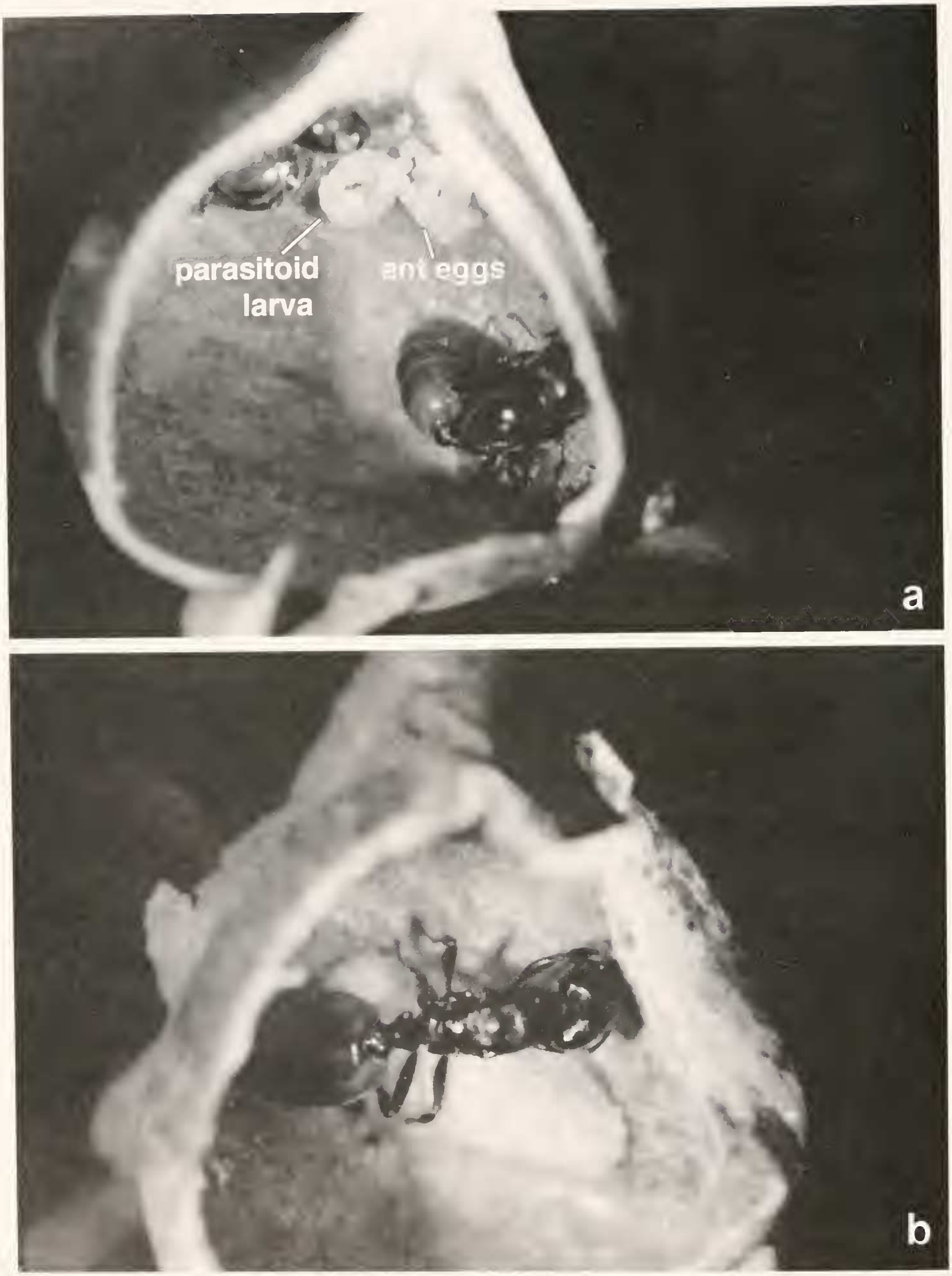

Fig. 1. *Trigastrotheca laikipiensis* Quicke sp. nov., life stages: a, mid instar larva feeding on *Cremastogaster nigriceps* eggs with foundress queen in lower right; b, *T. laikipiensis* sp. nov. cocoon in situ protected by *C. nigriceps* foundress queen.

Fig. 2. Late instar larva of *Trigastrotheca laikipiensis* Quicke sp. nov., feeding on well-developed *Crematogaster nigriceps* larva.

the key to the Old World genera of Braconinae of Quicke (1987).

The genus *Kenema* was erected based on a single male specimen from Sierra Leone (van Achterberg 1983), and subsequently a 2nd species from Senegal was described by van Achterberg and Sigwalt (1987). According to their diagnostic key, published in the same year that Quicke (1987) synonymized *Kenema* with *Trigastrotheca, Kenema* differs from the latter in that the 5th metasomal tergite completely lacks an apicomedial protuberance and is longer compared to the 4th; it also has less well developed anterolateral grooves on tergites 3–5, and fore wing vein r originates slightly more distally on the pterostigma. Based on our examination of much material in various collections, and additionally members of both sexes of the new species of *Trigastrotheca* described below, it is clear that the posterior margin of the 5th metasomal tergite is not always tridentate in *Trigastrotheca.* In males it is simple, though relatively a little longer than in most other genera, and in the case of the new species described here, can have a small sub-posterior medial hump that is presumably a reduced expression of the female's strong medial point. Further, the finely serrate apparent posterior margin of the 4th and 5th metasomal tergites produced by an overhang of the coriaceous sculptured dorsal surface over the true margin in the new species is closely similar to that in *Kenema serrata* van Achterberg & Sigwalt, suggesting that this might be a synapomorphy for the two species. Because of these observations, the synonymy of *Kenema* with *Trigastrotheca* originally proposed by Quicke (1987) is hereby supported.

Trigastrotheca laikipiensis Quicke, new species (Figs 2–4)

Holotype female.—Laikipia District, Kenya. Collected 11 July 2001 at Mpala Research Centre by M. Stanton. Found sealed within a swollen thorn of *Acacia drepanolobium* with a claustral colony of *Crematogaster nigriceps* ants. Bohart Museum of Entomogy; University of California; Davis, CA USA.

Paratypes.—2 ♀♀ and 1 ♂: Laikipia District, Kenya. Collected 20 July 2001 at Mpala Research Centre by M. Stanton. Found sealed within swollen thorns of *Acacia drepanolobium* occupied by claustral colonies of *Crematogaster mimosae* ants. BMNH.

Length of body, 4.3 mm, forewing 3.7mm, antenna 2.7mm and part of ovipositor exserted beyond apex of metasoma 1mm.

Head strongly transverse, densely setose; more or less uniformly coriaceous-rugulose. Antenna robust, with 26–27 flagellomeres. Terminal flagellomere robust and distinctly acuminate. Median flagellomeres marginally longer than wide. Height of clypeus: inter-tentorial distance: tentorio-ocular distance = 1.0:3.6:2.2. Face with distinct mid-longitudinal carina on somewhat protruding upper third. Width of head : height of eye : shortest distance between eyes = 2.8:1.0:1.6. Eyes with short sparse setae. Frons with strong mid-longitudinal ridge ending abruptly shortly before anterior ocellus. Posterior ocellar line : transverse diameter of posterior ocellus : shortest distance between posterior ocellus and eye = 4.4:1.0:3.7.

Mesosoma almost entirely coriaceous. Notauli well developed; mesoscutum with a weak but distinct mid-longitudinal ca-

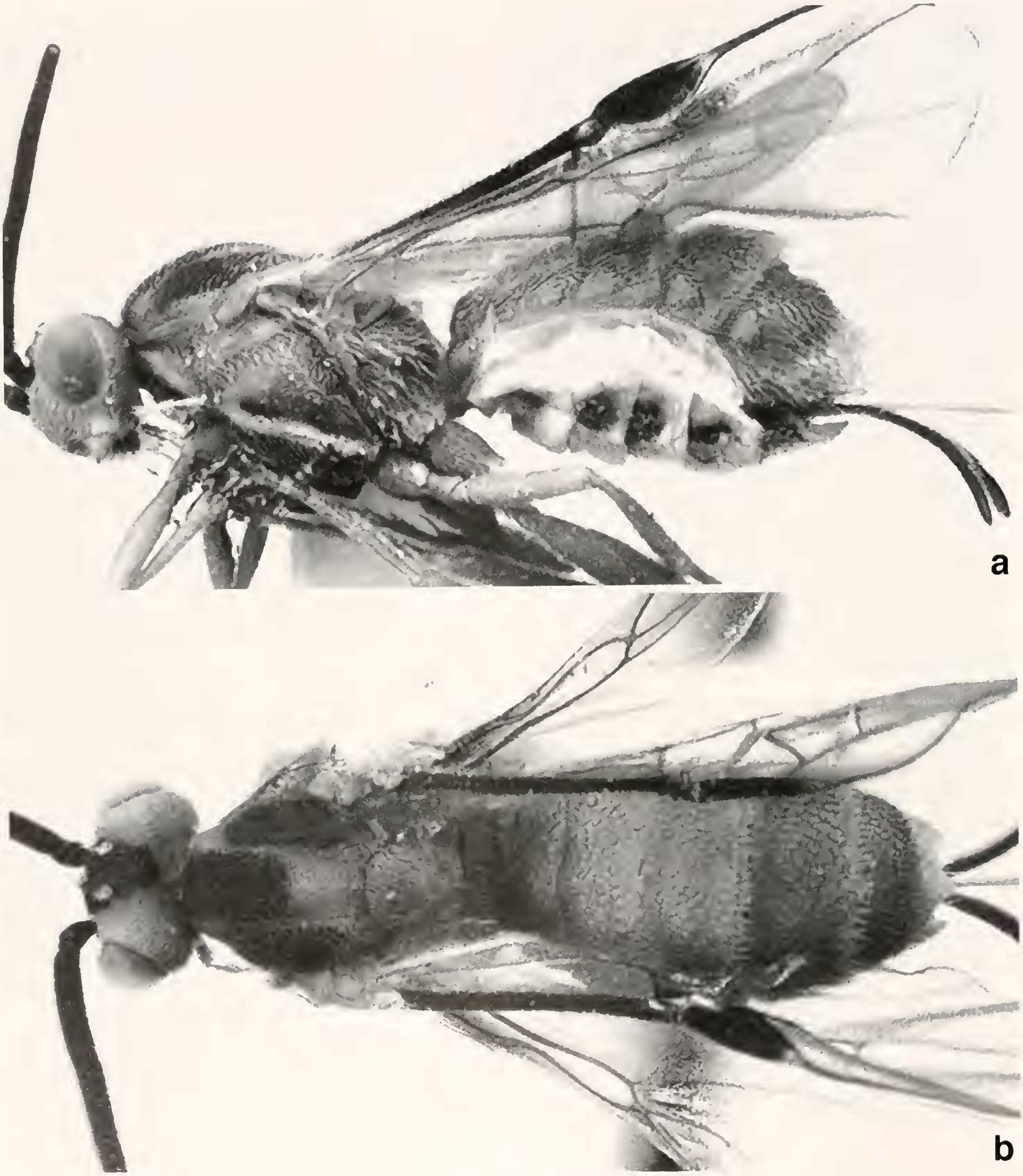

Fig. 3. Automontage® habitus pictures of *Trigastrotheca laikipiensis* Quicke sp. nov., female holotype: a, lateral aspect, b, dorsal aspect.

rina. Pronotum laterally with a deep crenulated curved groove and with strong sub-longitudinal striation below this. Mesopleuron with a weakly depressed broad mesopleural suture, and with an apparently weakly sclerotized almost complete sternaulus below this. Median area of metanotum with complete mid-longitudinal carina. Propodeum with a complete mid-longitudinal (sub-lamelliform) carina running within a distinct crenulated groove; with distinct straight sub-lateral carinae ending at level of spiracle just above a distinct strongly setose protuberance; with curved ('C'-shaped) crenulated groove below spiracle; posteriorly with a few distinct anteriorly-diverging short carinae.

Claws with small but distinctly pointed basal lobes. Lengths of fore femur : tibia : tarsus = 1.0:1.0:1.14. Lengths of hind femur : tibia : tarsus = 1.0:1.4:1.3. Hind femur very robust, 3.5 times longer than maximally deep.

Forewing veins 1-M and 1-SR+M meeting at an acute angle near wing margin, vein 1-SR short, forming an angle of 85° with C+SC+R. Lengths of veins r : 3-SR : SR1 = 1.0:1.36:5.0. Vein r arising 0.28–0.3 from the base of pterostigma. Pterostigma 3.2 times longer than broad. Lengths of veins 2-SR : 3-SR : r-m = 1.45:1.75:1.0. Vein 2-SR+M slightly longer than 1m-cu. Vein 3-CU1 forming a continuous curve with CU1b.

Metasoma strongly coriaceous. Tergites 3–5 with well developed antero-lateral triangular areas. Posterior margins of 3rd and 4th metasomal tergites appearing strongly dentate, but this is due to the strong coriaceous-rugose sculpture combined with a steep posterior margin such that the individual confluences of rugae, each of which bears a posteriorly-directed seta, overhangs the true posterior tergal margins. Posterior margin of 5th tergite of female with deep sub-median semicircular emarginations creating sharp medial point between them; lateral to emarginations border with fine serration. Ovipositor lacking pre-apical dorsal nodus and with no lower valve teeth visible at ×40; in lateral aspect strongly depressed at apex.

Coloration mostly ochreous yellow with variable dark markings (mark on top of head formed into two points anteriorly, large marks on the medial and lateral lobes of the mesoscutum, mesosternum and metasomal sternites), and with whitish, less sclerotized, longitudinal line along the position of the sternaulus (i.e. below the depressed part of the mesopleural suture). Antennae black; mandibles whitish with blackish tips; wing membrane weakly greyish, wing venation dark brown to blackish. Ovipositor pale brownish.

Variation.—Some paratypes are slightly less extensively marked with black or dark brown, one female paratype having dark spots antero-laterally on the propodeum. The male has the propodeum, scutellum and most of the mesoscutum except a small medio-posterior part, a mark on the middle of the 1st metasomal tergite, and small spots mediolaterally on the 3rd and 4th tergites blackish.

Notes.—Nine species of *Trigastrotheca* have been described previously: *T. inermis* (Guérin-Méneville) **comb. nov.** (on authority of C. van Achterberg) [*Spinaria inermis* Guérin-Méneville, 1848], *T. nigricornis* Cameron, *T. quickei* (van Achterberg), *T. romani* **nom. nov.** [= *Coelodontus costator*: Roman; = *Ichneumon costator* Thunberg a junior homonym of *Ichneumon costator* Donovan, 1810; see Yu & Horstman (1997)], *T. rugosa* (Szépligeti) **comb. nov.** [= *Bracon rugosa* Szépligeti; = *K. rugosa*: Quicke & Koch (1990)], *T. serrata* (van Achterberg & Sigwalt), *T. tricolor* Quicke & Ingram, *T. tridentata* (Enderlein) and *T. trilobata* Cameron.

The new species described here can be distinguished from all other described species of *Trigastrotheca* by its smaller size and colour pattern. The apparently closely-related *T. serrata* differs further in having the frons weakly convex, distinctly striate and without a mid-longitudinal carina, the mesoscutum with hardly any trace of notauli and without a mid-longitudinal ridge, the pronotum, propodeum and mesopleuron less heavily sculptured and the latter without mesopleural suture and sternaulus.

DISCUSSION

Parasites are known to have significant impacts on mature ant colonies in some systems (Morrison 1999, Feener 2000), but is not clear how common or ecologically important brood parasites of ant foun-

Fig. 4. Automontage® pictures of *Trigastrotheca laikipiensis* Quicke sp. nov., female holotype: a, head, anterior aspect; b, head, dorsal aspect; c, scutellum, propodeum and 1st two metasomal tergites; d, mesosoma, lateral aspect.

dresses might be. We have never observed *T. laikipiensis* within swollen thorns on trees occupied by mature colonies, suggesting that this parasite specializes on the brood of young foundress queens (also see Yu and Quicke 1997).

Many of the important elements of the host-parasite interaction described here remain obscure. The biology of *Trigastrotheca* has previously been unknown. Morphologically (presence of complete mid-longitudinal propodeal carina) the genus appears to be related to several that are associated with galls, such as *Simplicibracon* Quicke, *Testudobracon* Quicke and *Triaspidogastra* Granger. If this is the case then the group may historically be associated with distinct swellings on plant tissue, though in the other cases, oviposition appears to be through the plant tissue, and the ovipositor is typically furnished with a distinct dorsal nodus and apicoventral serrations (Quicke 1987). We do not know how eggs of *T. laikipiensis* enter the sealed chambers of claustral colonies of acacia-ants on *A. drepanolobium*, but it is likely that female wasps locate swollen thorns with foundress queens inside, and then pierce the thorn wall or the queen's entry seal to deposit an egg within the claustral chamber.

Within the Braconidae, parasitism of ants is rare, with only two previously known examples of its evolution. Members of the *Neoneurus* Haliday group of genera in the Euphorinae (previously treated as the subfamily Neoneurinae, but see Belshaw et al. 2001) are endoparasi-

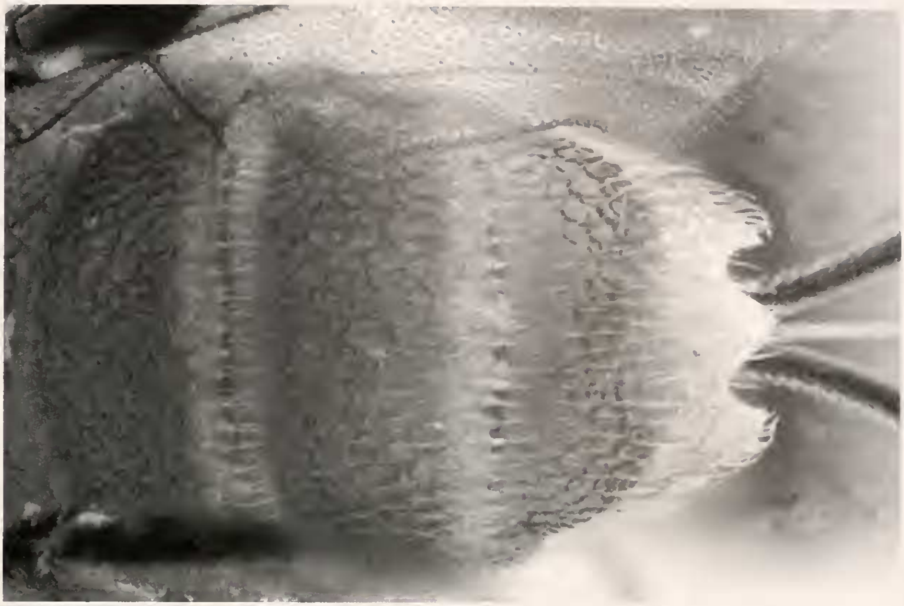

Fig. 5. Automontage® picture of *Trigastrotheca laikipiensis* Quicke sp. nov., female holotype: detail of posterior of metasoma, showing that dentation at posterior of 4th tergite is due to overhanging and seta-bearing sculpturation.

toids of adult worker ants (Shaw 1993). One species of the New World braconine genus *Compsobraconoides* Quicke parasitizes foundress queens of *Azteca* ants living in domatia in the plant *Cordia nodosa* Lam. (Boraginaceae) (Yu and Quicke 1997), but other members of this group have more typical biologies for the subfamily (Fortier and Nishida 2004, D. Janzen, unpublished data).

Given that the *Trigastrotheca* wasps probably gain protection from their foundress hosts through chemical crypsis or mimicry, it would be interesting to know whether there is any differentiation between individuals attacking the three ant species at our study sites. However, apart from some slight variation in coloration, all members of the individuals seen are morphologically very uniform, and therefore we currently consider them to represent a single species.

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